# Zooplankton research off Peru: A review

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## ARTICLE INFO

## ABSTRACT

A review of zooplankton studies conducted in Peruvian marine waters is given. After a short history of the development of zooplankton research off Peru, we review zooplankton methodology, taxonomy, biodiversity, spatial distribution, seasonal and interannual variability, trophodynamics, secondary production, and modelling. We review studies on several micro-, meso-, macro-, and meroplankton groups, and give a species list from both published and unpublished reports. Three regional zooplankton groups have been identified: (1) a continental shelf group dominated by *Acartia tonsa* and *Centropages brachiatus*; (2) a continental slope group characterized by siphonophores, bivalves, foraminifera and radiolaria; (3) a species-rich oceanic group. The highest zooplankton abundances and biomasses were often found between 4–6°S and 14–16°S, where continental shelves are narrow. Species composition changes with distance from the shore. Species composition and biomass also vary strongly on short time scales due to advection, peaks of larval production, trophic interactions, and community succession. The relation of zooplankton to climatic variability (ENSO and multi-decadal) and fish stocks is discussed in the context of ecological regime shifts. An intermediate upwelling hypothesis is proposed, based on the negative effects of low upwelling intensity in summer or extremely strong and enduring winter upwelling on zooplankton abundance off Peru. According to this hypothesis, intermediate upwelling creates an optimal environmental window for zooplankton communities. Finally, we highlight important knowledge gaps that warrant attention in future.

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## 1. Introduction

The coastal upwelling ecosystem off Peru hosts the world's largest single-species fisheries, which is sustained by wind-driven upwelling of nutrient-rich waters to the sunlit surface, where phytoplankton bloom at the base of highly productive pelagic food webs (Bertrand et al., 2005; see also Pennington et al., 2006). Many zooplankton eat phytoplankton, and are in turn preyed upon by fish larvae and many adult planktivorous fish. Conversely, certain zooplankton groups (e.g. medusae) also prey on fish eggs and larvae. Due to their intermediate position in the food web between primary producers and predators, zooplankton serves as a link between bottom-up climate-related control of phytoplankton and fish.

Here we present a short review of zooplankton research off Peru. We focused on meroplankton, macro-, meso-, and microzooplankton, but left the extensive literature on Peruvian ichthyoplankton for a separate review. We build on the short review by Guzmán and Carrasco (1996) of IMARPE ichthyo- and zooplankton studies. Montecino et al. (2006) and Pennington et al. (2006) provided overviews of biological–physical interaction processes off western South America, including several aspects of the Peruvian sector of the Humboldt Current System. More specific reviews of the Peruvian upwelling ecosystem were given by Arntz and Fahrbach (1991), Tarazona and Arntz (2001) and Tarazona et al. (2003), but the main emphasis was on benthic communities and fisheries stocks and zooplankton were mentioned only briefly. An extensive review of zooplankton in the eastern tropical Pacific, however, was recently published by Fernández-Álamo and Färber-Lorda (2006), who focused on large-scale surveys in the eastern tropical Pacific (e.g. EASTROPAC). Our review provides an overview of the work conducted off Peru. In particular, we (1) provide an overview and basis for comparison with other upwelling regions, by (2) summarizing all the literature available, much of which was found in unpublished reports and theses, and (3) identify gaps in our knowledge.

## 2. History of zooplankton research in Peru

Peruvian marine research was established in 1960 with the Instituto de Investigaciones de los Recursos Marinos (IREMAR) with the financial and technical support of FAO, which in 1964 changed its name to Instituto del Mar de Perú (IMARPE). IMARPE's

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initial mission was to compile scientific information about Peru's fish stocks to provide a scientific base for management decisions. With time, events affecting the stocks led to the realization that the scientific base had to be broadened to scale that were previously not regarded as necessary. This lesson was brought home by the catastrophic effects of El Niño's on the anchoveta fishery and Peru's continued dependence on this single-species fishery (Dickie and Valdivia, 1981).

Early zooplankton work concentrated on taxonomy and horizontal distribution (Vásquez, 1967; Alvarado, 1972; Gómez, 1972), especially of euphausiids (Santander, 1967; Santander and Sandoval de Castillo, 1969) and appendicularians (Fenaux, 1968). Additional work followed in the 70s during the International Decade of Ocean Exploration, which coincided with the initial decade of the Law of the Sea. The Law of the Sea emphasized that nations have rights to their coastal resources, including the right of exploration and research (Ancieta, 1981). Interest in the biological production in Peruvian coastal waters was high due to the prosperous anchovy-meal industry.

The international program CUEA (Coastal Upwelling Ecosystem Analysis, 1972–1980) was developed to study the physical, chemical, and biological drivers within upwelling ecosystems. It compared the upwelling systems of Oregon, Baja California, Peru, NW Africa, and Somalia. CUEA was conceived following the "Anton Bruun" Cruise off Peru in 1966 (e.g. Ryther et al., 1966; Ryther, 1967; Barber and Chavez, 1991). Under CUEA, interdisciplinary multiship studies were conducted off Peru during the JOINT-II expedition from March to October 1976 and March to May, 1977. Results were presented in a series of meetings (Barcelona, 1970; Investigaciones Pesqueras 35, 1, 1975; Marseille, 1973; Tethys 6, 1974; Kiel, 1975; Upwelling Ecosystems, 1978) and on the IDOE (International Decade of Ocean Exploration) International Symposium on Coastal Upwelling in Kiel, 1975.

Several cruises of the Institute of Oceanology, Russia, were conducted in 1974 (Vinogradov, 1977) to study the pelagic communities of tropical regions and their zones of intensive upwelling. The majority of the results are published in the journal Oceanology.

In 1975, the Peruvian-German Program PROCOPA (Programa Cooperativo Peruano-Alemán de Investigación Pesquera) was initiated, which lasted until 1985. Its main purpose was to support research in areas that could not be covered sufficiently by Peruvian scientists. Part of the program was the building of RV "Alexander Humboldt", which remains an important vessel in Peruvian fishery research in 1994, Germany funded time series sampling at stations off Paita and San José ("Fixed Coastal Stations Program", Table 2). Sampling at these stations is ongoing.

The bi-country project ICANE (Investigación Cooperativa de la Anchoveta y su Ecosistema) between Peru and Canada began in 1976 during severe changes in the fisheries. The goal was to identify causes of the recent decreases of the anchovy population, with the goal of predicting events in this system on time scales relevant to fishery management (Dickie and Valdivia, 1981). Results were published in Boletín Instituto del Mar del Perú-Callao, Vol. extraordinario (1981). These interdisciplinary programs improved Peruvian field work and data analysis and also established collaborations between Peruvian and foreign scientists.

During the 80s, most of the zooplankton papers published by IMARPE scientists (Table 3) focused on taxonomy (e.g. Santander et al., 1981a,b; Carrasco, 1989), species distributions, water mass indicator species (e.g. Véliz, 1981, 1985; Carrasco de Luyo, 1981; Dextre, 1983; Santander and Carrasco, 1985; Sandoval de Castillo, 1987), effects of El Niño on zooplankton biomass (Santander and Carrasco, 1985), and zooplankton biovolumes (1964–1985; Carrasco and Lozano, 1989). Non-IMARPE researchers published studies (Table 3) on community structure (e.g. Boyd and Smith, 1983; Timonin and Flint, 1986; Vinogradov et al., 1980), diel vertical migration (e.g. Judkins, 1980; Mackas et al., 1981; Smith et al., 1981b) and trophic ecology (e.g. Dagg et al., 1980; Boyd et al., 1980; Herman, 1984).

From the 90s to the present (2007), IMARPE zooplankton scientists have published papers on interaction between zooplankton and the environment (particularly El Niño; Aronés and Ayón, 2002; Castillo et al., 2005), species composition and abundance (Abanto, 2001), diel vertical migration (Escudero, 2003), and zooplankton time series relative to fish stock (Alheit and Niquen, 2004) or hydrographic variability (Gutiérrez et al., 2005; Ayón et al., 2004; Aronés et al., in press; Ayón et al., 2008). This work was supported by the European Community VECEP Program (1993–1999), which supported several fisheries surveys, and World Bank loans to purchase laboratory equipment (1999). In 1998 the research vessel "José Olaya Balandra" was donated by the Japanese government including sampling gear and laboratory equipment. CICESE (Mexico) provided funds from 2004 to 2005 for the analysis of zooplankton time series. In 2005, the multi-country project CENSOR was launched in Peru, funded by the European Union ("Climate variability and El Niño Southern Oscillation: Implications for natural coastal resources and management"; Argentina, Chile, Peru, France, Germany, Spain). CENSOR's zooplankton component focuses on trophodynamic impacts on the time series variability, especially in coastal areas.

**Table 2**
Summary of the main types of regular zooplankton surveys off Peru.

| Program | Method | Comment |
|---|---|---|
| Hensen Net Program | Hensen net (330 μm mesh, 60 cm diameter), towed vertically from 50 m to the surface. Determination of Zooplankton settlement volume → Additional oblique bongo hauls (330 μm mesh, 60 cm diameter) from 200 m to surface | Several times per year since 1964. Hundreds of stations located over the whole marine area off Peru |
| Fixed Coastal Stations Program | WP2 net (330 μm mesh, 50 cm diameter), horizontal subsurface tows → Since 2004, oblique bongo net samples have been regularly taken at the Fixed Coastal Stations (330 μm mesh, 60 cm diameter for the Callao transect, 330 μm mesh and 22 cm diameter for Paita and San Jose transects) from 200 m to the surface or from the bottom to the surface | Bimonthly since 1994. Stations located on three transects perpendicular to the coast off Paita, San José, and Callao |
| Intensive Cruises Program (CRIOS) | Experiments for secondary production and grazing, Multinet (330 μm mesh), WP2 net (330 μm mesh) oblique bongo net sampling, laser optical plankton counter | Twice a year since 2005. Stations located on three transects off Callao and inside Bahia de Independencia. Started in the context of the CENSOR project |

**Table 1**
Water masses found in surface waters off Peru.

| Water masses | Salinity | Temperature (°C) |
|---|---|---|
| Tropical Surface Water (TSW) | <33.8[a] | >25[b] |
| Equatorial Surface Water (ESW) | 33.8–34.8[b] | >20[b] |
| Subtropical Surface Water (SSW) | 35.1–35.7[a] | 18–27[b] |
| Cold Coastal Water (CCW) | 34.8–35.1[a] | 14–18[c] |

[a] Zuta and Guillén (1970).
[b] Gutiérrez et al. (2005).
[c] Morón (2000).

**Table 3**

Overview over selected publications on specific topics related to the zooplankton in marine waters off Peru.

| Topics | Main references |
|---|---|
| Biogeography, distribution, and ecology of specific taxa | Siphonophores (Bigelow, 1911; Véliz, 1985; Sears, 1953) |
| | Ostracods (Castillo, 2004; Castillo et al., 2005, 2007) |
| | Copepods (Alvarado, 1972; Gómez, 1972, 1982; Geynrikh, 1973; Santander et al., 1981b; Ayón et al., 1999; Abanto, 2001; Aronés, 2002; Aronés and Ayón, 2002) |
| | Amphipods (Carrasco de Luyo, 1981; Santander et al., 1981b; Carrasco, 1989; Aronés, 1997) |
| | Euphausiids (Santander, 1967; Santander and Sandoval de Castillo, 1969; Alvarado, 1972; Antezana, 1978; Santander et al., 1981a,b; Antezana, 2002a) |
| | Holoplanktonic molluscs (Quesquén and Guzmán, 1999; Quesquén, 2005) |
| | Chaetognaths (Bieri (1957, 1959); Alvarado, 1972; Santander et al., 1981a,b; Dextre, 1983; Sandoval de Castillo, 1987) |
| | Appendicularians (Fenaux, 1968) |
| | Zooplankton guides (Santander, 1981; Santander et al., 1981a,b) |
| | Horizontal distribution and biogeography (Vásquez, 1967; Beers et al., 1971; Vinogradov, 1977; Guillén, 1978; Santander et al., 1981a,b; Dextre, 1983; Timonin and Flint, 1986; Vasil'ev, 1991; Ayón et al., 1996; Ayón and Girón, 1996; Aronés and Ayón, 2001; Aronés et al., 2001; Quesquén, 2004; Aronés, 2004; Gutiérrez et al., 2005) |
| Vertical distribution | Judkins (1980), Sameoto (1981), Mackas et al. (1981), Smith et al. (1981a,b), Glebov (1982), Semenova et al. (1982) and Antezana (2002b) (for *Euphausia mucronata*); Escudero (2003) and Criales-Hernández et al. (2008) |
| Development of plankton communities | Mikheyev (1977a,b), Smith (1978), Vinogradov and Shushkina (1978), Vinogradov et al. (1980) and Boyd and Smith (1983) |
| Time series | Zooplankton volumes off Peru since 1964 (Carrasco and Lozano, 1989; Ayón et al., 2004) |
| | Hydrography and mesozooplankton abundance and diversity off Paita 1994–2004 (Aronés et al., in press) |
| El Niño | Dextre (1983), Santander and Carrasco (1985), Carrasco and Santander (1987), Aronés (1997), Gómez (1997), Ayón et al. (1999), Aronés and Ayón (2002) and Castillo et al. (2005) |
| Trophic ecology | Grazing and excretion (Cowles, 1978, 1979; Dagg et al., 1980; Boyd et al., 1980; Paffenhöfer, 1982; Arashkevich et al., 1982; Herman, 1984) |
| | Zooplankton productivity (Shushkina and Kislyakov, 1977) |
| | Functional characteristics of planktonic communities (Shushkina et al., 1978) |
| | Microzooplankton production (Sorokin, 1978; Tumantseva and Kopylov, 1985a) |

## 3. Study area – water masses, currents, and upwelling

The distribution of planktonic organisms is dependent on currents and water masses. The waters off Peru are part of the Humboldt Current System (HCS), which dominates most hydrodynamic processes off Chile and Peru (Fig. 1; cite reviews in PIO vol. 69). The Peru Coastal Current (PCC) flows equatorward, while the Peru–Chile Under-Current (PCUC) follows the shelf break towards the pole, and the Peru–Chile Counter-Current (PCCC) flows directly towards the south and veers to the west around 15°S (Penven et al., 2005). The flow of the PCC is strongest in austral winter, when equatorward winds are maximal (Bakun and Nelson, 1991; Echevin et al., 2004a,b; Croquette et al., 2005). It carries colder and saltier upwelled water to the north where they eventually become part of the South Equatorial Current (SEC).

Many oceanographic features vary seasonally and interannually, especially during EN. During "average" years, and especially during La Niña events, the Peruvian shelf is dominated by Cold Coastal Water (CCW, see Table 1), which is strongly influenced by coastal upwelling. Under normal conditions, upwelled waters originate from the PCUC (Echevin et al., 2004a,b). This upwelling of nutrient-rich waters sustains one of the most productive ecosystems of the world, with zooplankton biomasses which are among the highest recorded for large marine ecosystems in lower latitudes (Fernández-Álamo and Färber-Lorda, 2006). Plumes of upwelled water may extend several hundred km offshore at the
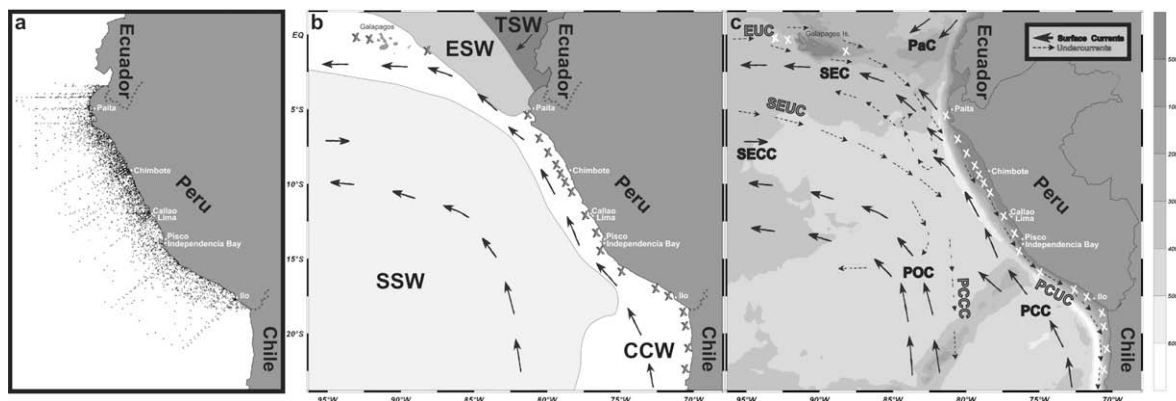


**Fig. 1.** Study area along the Peruvian coast showing zooplankton sampling stations covered since 1964 (Ayón et al., 2004, modified) (a), schematic distribution of characteristic surface water masses (b), and bathymetry with main currents (c). The approximate locations for main upwelling areas for nutrient-rich waters are indicated ("X"). According to Gunther (1936), Wyrtki (1963, 1967), Zuta and Guillen (1970), Tsuchiya (1981), Huyer et al. (1991), Strub et al. (1998), Schneider et al. (2003), Penven et al. (2005) and Croquette and Eldin (2006), modified. Water masses in b: CCW, Cold Coastal Water and mixed waters under the influence of upwelled cold waters; SSW, Subtropical Surface Water; ESW, Equatorial Surface Water; TSW, Tropical Surface Water. Currents in c: EUC, Equatorial Undercurrent or Cromwell Current; PaC, Panama Current; PCC, Peru Coastal Current, Chile–Peru Current, or Humboldt Current; PCCC, Peru–Chile Counter-Current; PCUC, Peru Coastal Undercurrent, Poleward Undercurrent (PUC), or Gunther Current; POC, Peru Oceanic Current, Oceanic Chile–Peru Current, or Oceanic Humboldt Current.

surface, leading to large-scale offshore blooms, but in general off-shore oceanic waters are warmer and contain less nutrients than nearshore upwelled waters. The upwelled and offshore PCC waters interact on several time scales, e.g. the alternation of upwelling and relaxation episodes, seasonal variability upwelling strength, and most drastically by EN. During EN, warm and low-salinity Equatorial Surface Water (ESW) and Tropical Surface Water (TSW) spread southward, and offshore PCC water reaches closer to the coast (Zuta and Guillen, 1970; Fiedler and Talley, 2006). Replacement of nutrient-rich upwelled water by warmer and more oligotrophic offshore water masses leads to drastic changes in pelagic ecosystems.

Sea surface temperatures (SST) increase towards the equator. In northern Peru, equatorward of 14°S, summer SSTs reach 26 °C, while to the south minimum summer SSTs are 17–18 °C (Zuta and Guillen, 1970). In central and sourthern Peru, in winter, SST varies from 13 to 17 °C, and the 19 °C isotherm is found north of 10°S. Stronger than seasonal SST changes, however, ENSO generates a huge interannual variability (Fig. 4). Spatial SST differences are caused by basin scale latitudinal and local (shelf width, water depth) components. The Peruvian shelf is <200 m deep and widest (65 nm) between 7°S and 10°S, and narrowest (3–5 nm) equatorward 7°S and polewardof 15°S (Zuta and Guillen, 1970).

# 4. Research topics

## 4.1. Sampling and survey development

IMARPE has always focused on fisheries. Zooplankton samples were a by-product of ichthyoplankton sampling, which was conducted on all surveys, be it pelagic, demersal or hydrographic surveys. Between 1961 and 2006 ~150 surveys were carried out with more than 10,000 samples collected. Surveys covered up to 500 km from the coast between 3°30′S and 18°20′S, although over 95% of the samples were collected within 100 km of the coastline (Fig. 1). Two types of standard surveys for zooplankton sampling have evolved with time (Table 2):

1. In the Hensen Net Program, zooplankton data have been collected since 1964 on Pelagic Fish, Demersal Fish and Oceanographic Surveys, where a Hensen net (330 μm mesh, 60 cm diameter) has been towed vertically from 50 m to the surface. After removal of large coelenterates and ichthyoplankton, the zooplankton settlement volume is measured (Carrasco and Lozano, 1989; Ayón et al., 2004). The stations are located on a predefined meander-shaped cruise track covering the whole coastal area of Peru, although the cruise track was sometimes modified. Zooplankton samples were only taken at stations where echograms indicated fish were present and fish trawling should also be conducted. Since 1996, additional zooplankton sampling has been conducted where distance between trawl positions was >20 nm.
2. In the Fixed Coastal Stations Program, on transects perpendicular to the coast near Paita, San José and Callao horizontal surface tows have been taken since 1994 with a WP2 net (Working Party 2; UNESCO, 1968; 330 μm mesh, 50 cm diameter). Additionally, since 2004, oblique bongo net tows (60 cm diameter, 300 μm mesh size; Table 2) have been included.

During a limited project in 1996/1997, vertically stratified samples with a closing net (200 μm mesh, 85 cm mouth diameter) were taken, usually from 100–50–25–10–0 m on two fixed stations near Callao (12°12.0′S, 077°18.0′W, Escudero, 2003) and Chimbote (09°20.4′S, 79°41.0′W). Since 2000, on Demersal Fish Surveys stratified samples have been taken with a multinet (Hydrobios, 330 μm mesh, 50 × 50 cm mouth size) from 200–150–100–50–10–0 m. More advanced sampling methods have recently been used during the Intensive Cruises Program (CRIOS) that was started under the CENSOR project (Table 2, Section 4).

## 4.2. Biodiversity

In general, knowledge of the taxonomy of the zooplankton fauna is poor, considering the amount of work invested into sampling (Table 2) and the ecological and economic importance of these ecosystems. Bigelow (1911) and later Sears (1953) worked on siphonophores collected by the US Steamer Albatross in 1904/1905. Santander et al. (1981a,b) catalogued 3 siphonophore, 31 copepod, 35 amphipod, 6 euphausiid, and 6 chaetognath species. Abanto (2001) presented a list of 152 copepod species from 54 genera collected on 15 cruises between 3°30′S and 14°S and 1980–1989. The zooplankton species in Table 4 were identified from the Fixed Coastal Stations Program since 1994, and since 1997 from material sampled in the Hensen Net Program. Previously existing keys have usually been used for identification, which often are based on material from other regions. Organisms have sometimes been mis-identified. For example, during the same expeditions the abundant *Calanus* species were called *Calanus chiliensis* (Sameoto, 1981) and *C. australis* (Santander et al., 1981b). Therefore, a careful taxonomic revision of the fauna of the southeast Pacific is required.

## 4.3. Spatial patterns

### 4.3.1. Horizontal distribution and abundance
Santander (1967) provided the first data on major taxa in surface samples from transects perpendicular to the coast between Callao and Chimbote (copepods, euphausiids, appendicularians, siphonophores, and pteropods). In 1987, Carrasco and Santander found that during normal conditions between 6°S and 12°S, copepods were most abundant, followed by siphonophores, chaetognaths, polychaetes, euphausiids, and amphipods. Other studies have found that the main zooplankton groups off Peru were copepods, euphausiids, and chaetognaths (Ayón and Girón, 1996, 1997; Ayón and Aronés, 1997a,b; Ayón et al., 1996; Ayón and Girón, 2004). Off Paita and San José, ca. 98% of the zooplankton were crustaceans, copepods being by far the most abundant group (Gutiérrez et al., 2005).

Santander (1981) studied the zooplankton in an important upwelling area from Pisco to San Juan, in autumn 1976 and 1977. She concluded that food quality and concentration were regulating the zooplankton composition, being low primary production associated to the dominance of euryphagous or carnivorous species, with less herbivourous species. Santander (1981), defined three major zooplankton groups: (1) continental shelf (dominated by *A. tonsa* and *C. brachiatus*); (2) continental slope (siphonophores, bivalves, foraminifera, and radiolaria), (3) oceanic group (*Mecynocera clausi*, *Pleuromamma gracilis*, *Scolecithrix danae*, *Lucicutia flavicornis*, *Euchaeta marina*, *Euchirella bella*, *Oithona plumifera*, *Calocalanus pavo*, *Temora stylifera*, *T. discaudata*, *Nannocalanus minor*, *Eucalanus subtenuis*, *Acrocalanus* sp., *Corycaeus* sp., *Oithona* sp., *Oncaea* sp., *Sapphirina* sp., *Corycella* sp., *Copilia* sp.). Sameoto (1981) confirmed this species composition changes with distance from the shore, but noticed a high variability in species composition and biomass that can occur on daily time.

Planktonic ecosystems of the PCC under the influence of upwelled Cold Coastal Waters (CCW) differ markedly from the subtropical waters to the west by their high concentration of life (fish, birds, mammals, etc.) and by their huge biomass (Ayón et al., 2004). However, a recent analysis of historical data indicates that within the CCW, higher biovolumes are found offshore, prob-

**Table 4**

List of species identified in Peruvian zooplankton samples (Ayón et al., 2008, status of 2006). References: (1) IMARPE, unpublished; (2) Sears (1953); (3) Véliz (1985); (4) Santander et al. (1981a,b); (5) Quesquén (2005); (6) Castillo (2004); (7) Abanto (2001); (8) Gómez (1982); (9) Carrasco and Santander (1987); (10) Carrasco (1989); (11) Aronés (1997); (12) Santander (1967); (13) Dextre (1983); (14) Sund (1964); (15) Sandoval de Castillo (1987); (16) Fenaux (1968).

**Cnidaria**
Solmundella bitentaculata 1
Aeginura grimaldii 1
Aequorea coerulescens 1
Aequorea macrodactyla 1
Bougainvillia superciliaris 1
Bouganvillia fulva 1
Heterotiara anonyma 1
Obelia sp. 1
Phialidium uchidai 1
Cladonema sp. 1
Euphysa tentaculata 1
Sarsia eximia 1
Sarsia sp. 1
Cunina octonaria 1
Cunina frugifera 1
Cunina peregrina 1
Cunina globosa 1
Cunina tenella 1
Cunina duplicata 1
Solmissus incisus 1
Cytaeis tetrastyla 1
Geryonia proboscidalis 1
Liriope tetraphylla 1
Halicreas minimum 1
Hydractinia sp. 1
Eucheilota menoni 1
Tiaricodon coerulens 1
Amphinema sp. 1
Leuckartiara octona 1
Leuckartiara zacae 1
Stomotoca pterophylla 1
Stomotoca atra 1
Halitholus intermedia 1
Porpita porpita 1
Vellela velella 1
Pochella polynema 1
Aglaura hemistoma 1
Rhopalonema funerarium 1
Rhopalonema velatum 1
Sminthea eurygaster 1
Amphogona apicata 1
Pantachogon sp. 1
Pegantha laevis 1
Pegantha martagon 1
Pegantha clara 1
Pegantha triloba 1
Solmaris sp. 1
Chromatonema crythrogonon 1
Ectopleura dumortieri 1
Ectopleura sacculifera 1
Atolla wyvillei 1
Nausithoe punctata 1
Nausithoe rubra 1
Pelagia noctiluca 1
Chrysaora plocamia 1
Periphylla periphylla 1
Stomolophus meleagris 1
Phacellophora camtschatic 1
Abyla peruana 2
Ceratocymba leuckarti 1
Abylopsis tetragona 3
Abylopsis eschscholtzi 3
Bassia bassensis 1
Enneagonium hyalinum 1
Nanomia cara 1
Agalma elegans 3
Athoribia rosacea 1
Sulculeolaria biloba 1
Sulculeolaria chuni 1
Sulculeolaria quadrivalvis 1
Sulculeolaria turgida 1
Chelophyes appendiculata 1
Chelophyes contorta 1
Dyphes bojani 1

Dyphyes dispar 3
Eudoxoides mitra 1
Eudoxoides spiralis 3
Lensia campanella 1
Lensia conoidea 1
Lensia cossack 1
Lensia fowleri 1
Lensia hotspur 1
Muggiaea atlantica 4
Muggiaea kochii 3
Hipopodius hippopus 1
Physophora hydrostatica 1
Rosacea plicata 1
**Ctenophora**
Bolinopsis infundibulum 1
Velamem sp. 1
Pleurobrachia pileus 1
Hormiphora plumosa 1
Beroe cucumis 1
**Annelida**
Pelagobia longicirrata 1
Tomopteris sp. 1
**Mollusca**
Protatanta souloyeti 5
Oxygyrus keraudreni 5
Atlanta turriculata 5
Atlanta helicinoides 1
Atlanta lesueuri 5
Atlanta peroni 5
Atlanta gaudichaudi 5
Atlanta inclinata 5
Carinaria lamarcki 5
Cardiapoda placenta 1
Pterotrachea hippocampus 5
Pterotrachea coronata 5
Firoloida desmaresti 5
Limcina bulimoides 5
Limacina inflata 5
Limacina trochiformis 5
Cavolinia inflexa 5
Cavolinia longirostris 5
Cavolinia uncinata 5
Diacria quadridentata 5
Clio pyramidata 5
Creseis acicula 5
Creseis virgula 5
Hyalocylis striata 5
Cymbulia sibogae 5
Desmopterus papillo 5
Peraclis apacifulva 1
Peraclis reticulata 1
Glaucus sp. 1
Phillirhoe bucephala 1
Cephalopyge trematoides 1
**Branchiopoda**
Penilia avirostris 1
Pleopis polyphemoides 1
Evadne espinifera 1
Evadne nordmanni 1
Pseudoevadne tergestina 1
**Ostracoda**
Archiconchoecia striata 6
Halocypris inflata 6
Euconchoecia aculeata 6
Euconchoecia chierchae 6
Conchoecetta giesbrechti 6
Conchoecia aff magna 6
Disconchoecia tamensis 6
Metaconchoecia inflata 6
Metaconchoecia kyrtophora 6
Mataconchoecia teretivalvata 6
Orthoconchoecia agassizi 6
Orthoconchoecia striola 6
Porroecia parthenoda 6
Porroecia porroecia pacifica 6

Porroecia pseudoparthenoda 6
Proceroecia decipiens 6
**Copepoda**
Acartia danae 7, 8
Acartia erytraea 7
Acartia negligens 7
Acartia lilljeborgii 1
Acartia tonsa 7, 8
Aetideus armatus 7
Aetideus giesbrechti 7
Euaetideus bradyi 7, 8
Euchirella bella 7, 8
Euchirella messinensis 1
Haloptilus acutifrons 7
Haloptilus ornatus 7
Haloptilus oxycephalus 7
Haloptilus sp. 7
Calanus australis 7, 8
Calanus chilensis 8
Calanus darwinii 1
Calanus tenuicornis 7
Canthocalanus pauper 1
Nannocalanus minor 7
Neocalanus robustior 7
Undinula darwinii 7
Undinula sp. 7
Candacia bipinnata 7
Candacia catula 7, 9
Candacia curta 7, 8
Candacia simplex 1
Candacia pachydactyla 7
Paracandacia truncata 7
Centropages brachiatus 7, 8
Centropages elongatus 7
Centropages furcatus 7
Centropages gracilis 7
Clausocalanus arcuicornis 7, 9
Clausocalanus sp. 7
Clausocalanus jobei 1
Clausocalanus furcatus 1
Clytemnestra rostrata 7, 8
Clytemnestra scutellata 7
Corycaeus auronitens 1
Corycaeus dubius 8
Corycaeus catus 7
Corycaeus crassiusculus 7
Corycaeus flaccus 7
Corycaeus furcifer 7
Corycaeus gibulus 10
Corycaeus lautus 1
Corycaeus limbatus 1
Corycaeus longistylis 7
Corycaeus robustus 7
Corycaeus speciosus 7
Corycaeus spp. 7
Farranula gibbula 7
Microsetella gracilis 7
Microsetella rosea 7
Eucalanus inermis 7, 8
Eucalanus elongatus 1
Paraeucalanus attenuatus 7
Rhincalanus cornutus 7
Rhincalanus nasutus 7, 8
Subeucalanus crassus 7
Subeucalanus mucronatus 7
Subeucalanus subcrassus 7
Euchaeta acuta 7, 10
Euchaeta indica 7
Euchaeta longicornis 7
Euchaeta media 1
Euchaeta plana 7
Euchaeta rimana 7
Euchaeta sp. 7
Euterpina acutifrons 10; 7
Heterorhabdus lobatus 1

**Table 4** (*continued*)

| | | |
|---|---|---|
| *Heterorhabdus papilliger* 7 | *Temora discaudata* 7 | *Pagurus* sp. 1 |
| *Lucicutia flavicornis* 7, 8 | *Temora stylifera* 1 | *Blefaripoda* sp. 1 |
| *Lucicutia gaussae* 7 | *Tharybis* sp. 7 | *Lepidopa* sp. 1 |
| *Mecynocera clausii* 7, 8 | ***Amphipoda*** | *Emerita analoga* 1 |
| *Pleuromamma borealis* 7, 8 | *Anapronoe* sp. 1 | *Cancer setosus* 1 |
| *Pleuromamma abdominalis* 1 | *Dairella* sp. 1 | *Platyxanthus* sp. 1 |
| *Pleuromamma gracilis* 8 | *Hyperioides sibaginis* 10, 11 | *Libinia* sp. 1 |
| *Pleuromamma piseki* 7 | *Phronimopsis spinifera* 10, 11 | ***Euphausiacea*** |
| *Pleuromamma xiphias* 7 | *Hyperia medusarum* 10 | *Euphausia diomedae* 1 |
| *Oithona* sp. 7 | *Hyperietta vosseleri* 11 | *Euphausia mucronata* 12 |
| *Oithona atlantica* 1 | *Hyperietta luzoni* 11 | *Euphausia tenera* 12 |
| *Otihona fallax* 7 | *Hyperietta stephenseni* 11 | *Euphausia eximia* 12 |
| *Otihona nana* 1 | *Hyperiodes longipes* 11 | *Euphausia distinguenda* 12 |
| *Otihona plumifera* 7, 8 | *Hyperoche* sp. 1 | *Euphausia lamelligera* 12 |
| *Oithona setigera* 7, 8 | *Lestrigonus bengalensis* 11 | *Euphausia mutica* 1 |
| *Otihona similis* 10 | *Lestrigonus macrophthalmus* 11 | *Nyctiphanes simplex* 12 |
| *Paraoithona parvula* 7 | *Lestrigonus shoemackeri* 11 | *Nematoscelis tenella* 1 |
| *Paraoithona* sp. 7 | *Lestrigonus schizogeneios* 11 | *Nematoscelis gracilis* 1 |
| *Lubbockia squillimana* 7 | *Themistella fusca* 11 | *Nematoscelis flexipes* 1 |
| *Oncaea conifera* 7, 8 | *Lanceola* sp. 1 | *Stylocheiron affine* 1 |
| *Oncaea venusta* 7 | *Anapronoe* sp. 1 | *Stylocheiron carinatum* 1 |
| *Pachysoma dentatum* 7 | *Brachyscelus crusculum* 10, 11 | *Stylocheiron elongatum* 1 |
| *Acrocalanus gracilis* 7 | *Lycaea* spp. 11 | *Nematobrachium flexipes* 1 |
| *Acrocalanus monachus* 9 | *Pseudolycaea* sp. 1 | ***Mysida*** |
| *Acrocalanus armatus* 9 | *Thamneus* sp. 1 | *Heteromysis* sp. 1 |
| *Acrocalanus* sp. 7 | *Tryphana malmi* 11 | *Archaeomysis* sp. 1 |
| *Calocalanus pavo* 7 | *Lycaeopsis themistoides* 10, 11 | *Mysidopsis* 1 |
| *Calocalanus plumulosus* 7 | *Oxycephalus piscator* 10, 11 | *Siriella* sp. 1 |
| *Paracalanus parvus* 7, 8 | *Oxycephalus armatus* 10 | *Gybberithrops* sp. 1 |
| *Otihona plumifera* 7, 8 | *Oxycephalus clausi* 1 | *Metamysidopsis pacifica* 1 |
| *Otihona setigera* 7, 8 | *Simorhynchotus antenarius* 10 | ***Chaetognatha*** |
| *Parvocalanus* sp. 7 | *Calamorhynchus* sp. 1 | *Khronitta pacifica* 1 |
| *Phaenna spinifera* 7 | *Cranocephalus* sp. 1 | *Khronitta subtilis* 13 |
| *Calanopia* sp. 1 | *Rhabdosoma armatum* 1 | *Pterosagitta draco* 13 |
| *Labidocera acuta* 7 | *Streetsia* sp. 1 | *Sagitta bedoti* 14 |
| *Labidocera acutifrons* 7 | *Turbegella* sp. 1 | *Sagitta decipiens* 15 |
| *Labidocera* sp. 7 | *Glossocephalus* sp. 1 | *Sagitta enflata* 13 |
| *Labidocera pavo* 1 | *Leptocotis spinifera* 11 | *Sagitta ferox* 14 |
| *Pontella* sp. 1 | *Rhabdosoma minor* 11 | *Sagitta hexaptera* 15 |
| *Pontellina plumata* 7, 8 | *Paraphronima gracilis* 11 | *Sagitta minima* 13 |
| *Pontellopsis armata* 7 | *Thyropus diaphanus* 11 | *Sagitta maxima* 1 |
| *Pontellopsis perpicans* 1 | *Euscelus robustus* 11 | *Sagitta neglecta* 14 |
| *Pontellopsis regalis* 1 | *Schizoscelus ornatus* 11 | *Sagitta pacifica* 1 |
| *Pseudodiaptomus* sp. 7 | *Phronima sedentaria* 10 | *Sagitta peruviana* 14 |
| *Copilia miriabilis* 7 | *Phronimella elongata* 10, 11 | *Sagitta pulchra* 14 |
| *Copilia quadrata* 1 | *Phronima dunbari* 11 | *Sagitta regularis* 13 |
| *Sapphirina angusta* 1 | *Phronima colleti* 1 | ***Thaliacea*** |
| *Sapphirina auronitens* 7 | *Phrhonima bowmani* 11 | *Cyclosalpa bakeri* 1 |
| *Sapphirina darwinii* 7 | *Phrosina semilunata* 11 | *Helicosalpa komaii* 1 |
| *Sapphirina gastrica* 7 | *Anchylomera* sp. 1 | *Iasis zonaria* 1 |
| *Sapphirina gemma* 7 | *Primno macropa* 11 | *Pegea confoederata* 1 |
| *Sapphirina intestinata* 7 | *Amphithyrus sculpturatus* 11 | *Ritteriella picteti* 1 |
| *Saphirina iris* 1 | *Hemityphis tenuimanus* 11 | *Salpa fusiformis* 1 |
| *Sapphirina metalina* 7 | *Platyscelus* sp. 1 | *Thalia democratica* 1 |
| *Sapphirina nigromaculata* 7 | *Tetrathyrus forcipatus* 11 | *Thetys vagina* 1 |
| *Sapphirina opalina* 7 | *Parapronoe parva* 10 | *Weelia cylindrica* 1 |
| *Sapphirina ovatolanceolata* 7 | *Sympronoe* sp. 1 | *Doliolum gegenbauri* 1 |
| *Sapphirina* spp. 7 | *Eupronoe maculata* 11 | *Doliolum denticulum* 1 |
| *Sapphirina stellata* 7 | *Scina* sp. 1 | *Doliolum nationalis* 1 |
| *Amallothrix* sp. 7 | *Vibilia armata* 11 | ***Appendicularia*** |
| *Scaphocalanus echinatus* 7 | *Vibilia chuni* 11 | *Oikopleura dioica* 16 |
| *Scaphocalanus* sp. 7 | ***Decapoda*** | *Oikopleira fusiformis* 16 |
| *Scolecithricella abyssalis* 7 | *Solenocera* sp. 1 | *Oikopleura albicans* 16 |
| *Scolecithricella aupopecten* 7 | *Penaeus stylirostris* 1 | *Oikopleura cophocerca* 16 |
| *Scolecithricella bradyi* 7, 8 | *P. vannamei* 1 | *Oikopleura intermedia* 16 |
| *Scolecithricella dentata* 7 | *P. californicus* 1 | *Oikopleura longicauda* 16 |
| *Scolecithricella minor* 7 | *P. occidentalis* 1 | *Oikopleura rufescens* 16 |
| *Scolecithricella* spp. 7 | *Sergestes* sp. 1 | *Stegosoma magnum* 16 |
| *Scolecithrix danae* 7 | *Lucifer* sp. 1 | ***Cephalochordata*** |
| *Scolecithricella spinipedata* 7 | *Callianassa* sp. 1 | *Branchiostoma elongatum* 1 |
| *Scottocalanus* sp. 7 | *Callichirus* sp. 1 | |
| *Temeropia mayumbaensis* 7 | *Pleuroncodes monodon* 1 | |

ably due to stronger predation nearshore and low biovolumes in freshly upwelled water (Ayón et al., 2008). Also, there is a clear north–south pattern, with high biovolumes mainly between 4°S and 6°S and again poleward of 14°S. These high biovolume areas

are characterized by a narrow continental shelf (18–28 km) (Santander, 1981; Carrasco and Lozano, 1989; Ayón et al., 2004). The high biovolumes in the north may be due to the influence of the ESW, which have larger species and higher diversity (Ayón, 1999)

than CCW. On the other hand, the number of abundant tropical species greatly decreases toward the coast. In the coastal areas under influence of CCW, large neritic herbivores like *Calanus australis* and *Eucalanus inermis* may grow in mass (Geynrikh, 1973). Off northern and central Peru, euphausiids were less but the remaining mesozooplankton were more abundant (Gunther, 1936).

EN alters mesozooplankton diversity, distribution, and abundance. An increase in diversity is caused by the intrusion of tropical species in the central and southern Peruvian coast (Santander and Carrasco, 1985; Carrasco and Santander, 1987; Carr, 2003). Work off northern Peru during EN shows the intrusion of warm waters with warm water species such as *Centropages furcatus* (Santander et al., 1981b; Aronés et al., 2001). The 1982/1983 EN caused an increase in zooplankton biomass, especially gelatinous species, and diversity (Santander and Carrasco, 1985). In contrast, there was a pronounced decrease in meroplanktonic larvae and ichthyoplankton in the coastal waters during EN.

Specific attention on the regional and seasonal distribution of certain taxonomic groups was drawn by Véliz (1981), who identified ten species of siphonophores between 5°47′ and 9°13′ up to 260 km offshore, and by Castillo (2004) and Castillo et al. (2007) who studied the distribution of 15 ostracod species. During the 1998 EN ostracod species shifted south and their distributions showed positive or negative correlations with salinity and distance to shore.

Some species can be used as water masses indicators (Gómez, 1972; Geynrikh, 1973; Aronés, 2002; Castillo, 2004). Sandoval de Castillo (1987) used chaetognaths as water mass indicators, with *Sagitta bedoti*, *S. neglecta*, *S. peruviana*, and *S. pulchra* associated in ESW, and *S. ferox*, *S. regularis* and *Khronitta pacifica* in SSW. Carrasco and Santander (1987) showed that the copepods *Centropages furcatus*, *Acrocalanus gracilis*, and *A. monachus* were typical in ESW, while CCW species were *Clausocalanus arcuicornis*, *Acartia tonsa*, *Oithona plumifera*, *Paracalanus parvus*, *Centropages brachiatus*, and *Eucalanus inermis*. A recent study conducted off northern Peru (Gutiérrez et al., 2005) recognized several copepod species as indicators of SSW: *Acartia danae*, *Calocalanus pavo*, *Ishnocalanus plumulosus*, *Mecynocera clausii*, and *Oncaea conifera*. Abanto (2001) related the distribution of 152 copepod species to hydrographic data between 3°30′S and 14°S between 1980 and 1989. Examples are presented in Fig. 5. Thus, *Acartia tonsa*, *Calanus australis*, *Clausocalanus* sp., *Paracalanus parvus* are apparently eurythermal and euryhaline and not water mass specific, while *Subeucalanus crassus*, *Sapphirina darwinii*, *Pleuromamma abdominalis* were restricted to SSW, and *C. brachiatus*, *E. inermis*, *Euaetideus bradyi* could be used as indicator species for CCW. During EN, *Centropages furcatus* shifts south and replaced the CCW species *C. brachiatus* and *Eucalanus inermis* (Abanto, 2001). The shift between *C. brachiatus* (non-EN) and *C. furcatus* (EN) was also noticed by Gutiérrez et al. (2005), who related hydrographic parameters to changes in microphytoplankton, mesozooplankton (volume, abundance, and species richness), ichthyoplankton and macrozoobenthos in surface samples collected between 1994 and 2004 on fixed stations off central Peru. They found notable changes in species composition and richness associated with the 1997/1998 EN.

### 4.3.2. Vertical distribution and migration

The vertical distribution of zooplankton is controlled by their nutritional and physiological requirements; therefore, the structure of the water column with its gradients of temperature and salinity is important. Furthermore, in the Eastern Tropical Pacific, a subsurface OMZ (Pennington et al., 2006) has a profound impact on the distribution of pelagic animals and limits the space available for aerobic life. The upper limit of the OMZ depth is often identified as the depth of the 0.5 ml $L^{-1}$ (Escribano et al., 2000) or 1 ml $L^{-1}$ (Hidalgo et al., 2005; Criales-Hernández et al., 2008) oxygen isopleth. In regions of coastal upwelling, hypoxic water can reach to

within a few meters of the surface (Wyrtki, 1966; Judkins, 1980; Escribano et al., 2004). Not many studies have been conducted on the vertical distribution of zooplankton off Peru. Only during international cruises have closing nets, pumps and electronic plankton counters been used (Mackas et al., 1981). Judkins (1980) pumped samples down to 85 m at three stations at the shelf break, over the continental slope, and further offshore. The OMZ appeared to have been the single most important environmental factor structuring and modifying the vertical distribution of zooplankton over the shelf and slope off central Peru. Most mesozooplankton did not occur below the 0.1 ml $L^{-1}$ oxygen isopleth. Onshore shoaling of the OMZ resulted in high near-surface concentrations of mesozooplankton relative to offshore stations. Semenova et al. (1982) described the vertical and horizontal distribution of 37 mesozooplankton species along transects between 7°S and 15°S. Only two species were able to occupy the OMZ: *Eucalanus inermis*, which other studies have shown can with stand 12 h of anoxia (Judkins, 1980; Boyd et al., 1980), and *Euphausia mucronata* (Antezana, 2002a). A thickening of the surface oxygenated layer occurs during EN, and is accompanied by increased vertical migration and habitat expansion for many zooplankton and fish species (Escribano et al., 2004).

Diel vertical migration (DVM) was first demonstrated off Peru by Antezana (1978, 2002a,b). He showed that larvae and juveniles of *Euphausia mucronata* are always in the surface layer, while the adults spend days in the OML and migrate to the surface at night. Smith et al. (1981b) studied the vertical migrations of three copepod families with a 5 m resolution (Oncaeidae, Oithonidae, small Calanoida). The OMZ established a distinct lower boundary. During day-time, all three groups accumulated above the oxycline, while at night, small Calanoida were always higher in the water column than Oncaeidae. These daily excursions seemed sufficient to expose Oncaeidae to onshore/poleward flow by day and offshore/equatorward flow at night. Restriction to the upper 20 m above the OMZ likely influences the onshore–offshore distribution of species (Smith et al., 1981a). Boyd et al. (1980) observed that *Eucalanus inermis*, *Calanus australis*, and *Centropages brachiatus* show different patterns of DVM inshore and offshore, not apparently related to the OMZ. All three species left the upper 5 m during the day inshore, but offshore they remained at the surface both in day and night even though the surface oxygenated layer is thicker offshore. Santander et al. (1981a) found that many mesozooplankton can tolerate oxygen concentrations down to ~0.5 ml $L^{-1}$, but concentrations <0.2 ml $L^{-1}$ have drastic effects on most taxa. They also found that *Eucalanus inermis*, *Euaetideus bradyi*, *Rhincalanus nasutus*, amphipods, and ostracods occur mainly between 50 and 100 m, where the oxygen content was <0.5 ml $L^{-1}$. Using a closing net off Callao during three 48 h-periods, Escudero (2003) distinguished four types of migration, with species: (1) spending day at depth and coming to the surface between dusk and midnight; (2) not-migranting; (3) migranting several times each 24 h; and (4) reverse migrating, swimming up in the day and down at night, as in *Lucicutia flavicornis*. Environmental conditions modified the migrations, as O₂ concentrations <0.5 ml $L^{-1}$ were limiting for most taxa.

### 4.4. Time series: seasonality and interannual variability

Temporal variation of zooplankton abundance can occur as a result of both biological and physical processes. Biological variations occur at a time scale of weeks, associated with the life cycle of zooplankton organisms, and on a diurnal time scale associated with vertical migration. Physical variations can be seasonal and interannual, or also may occur as a result of onshore–offshore and alongshore advection, on a time scale of days. Changes in cross-shelf advection have been observed on a fixed station during 15 days of daily sampling (Smith et al., 1981a). During periods of surface

onshore flow, oceanic species were observed, while during offshore flow, coastal species dominated.

Seasonal variability is driven by changes in wind speed and direction, which affect upwelling intensity and coastal circulation. Anchovies and other species release larvae seasonally (Santander and Flores, 1983). Such spawning seasonality suggests that favourable pelagic conditions may also be seasonal. Upwelling off Peru is more intense in winter (Bakun and Nelson, 1991; Echevin et al., 2004a,b; Croquette et al., 2005; Aronés et al., in press). Since primary and secondary production is supported by upwelling nutrient-rich upwelled cold water, maximum phyto- and zooplankton abundances should occur in winter. However, Ayón et al. (2004) found peak zooplankton volumes in spring, especially during the 1960s (Fig. 2). Zooplankton volumes were higher in spring except during the 90s when no seasonal trend was evident. Aronés et al. (in press) analysed the seasonality of zooplankton abundance off Paita (Fig. 2). They generally found highest total abundances in spring and autumn, under moderate upwelling conditions. These observations may suggest that "intermediate-strength upwelling" is favourable for zooplankton, with winter upwelling too strong and summer upwelling too weak. Although coastal upwelling was more intense in winter, zooplankton abundance off Paita was at minimum during winter, and thus displayed a positive correlation with temperature (Aronés et al., in press). Studies off Chile have shown that intermediate monthly wind strengths, with alternating periods of upwelling and relaxation, may best sustain phytoplankton blooms off Chile (Echevin et al., 2004b) and successful recruitment of Peruvian pelagic fish stocks (Walsh et al., 1980; Mendelssohn and Mendo, 1987; Cury and Roy, 1989). Similar concepts have also been called the "optimal environmental window" (Cury and Roy, 1989; Sugimoto and Tadokoro, 1998) or "optimal stability window" (Gargett, 1997). We suggest that the dome-shaped relationship between wind-induced turbulence and zooplankton biomass has an important influence on zooplankton productivity off Peru (Aronés et al., in press), although the dominating mechanisms and processes are not yet clear. Cury and Roy (1989) suggested that strong winds decrease recruitment success by inducing turbulence that hampers the location of zooplankton prey by fish larvae off Peru. This idea is a restatement of "Lasker's hypothesis" (Lasker et al., 1970; Lasker, 1975; Lasker and Smith, 1977) which proposes that strong turbulent mixing (beyond an "optimum") associated with strong wind and coastal upwelling destroys vertical stratification and the prey patchiness required for optimal larval feeding. Under the "optimal window" hypothesis, intermediate upwelling intensity supplies nutrients but below intensity levels where harmful processes become important, such as horizontal advection and the break-up of vertical aggregation layers.

On the other hand, recent studies suggest that aggregations of zooplankton and fish larvae can be formed by vertical currents (Franks, 1992; Genin et al., 2005). In this case increased vertical turbulence may increase predation intensity by aggregating organisms that are dispersed horizontally, but are able to maintain their depth, such as zooplankton and fish larvae (Hardy, 1936; Franks, 1992; Genin et al., 2005). Increased wind and turbulence could also require increased effort to maintain depth, thus leaving less energy for growth and reproduction (Kloppmann et al., 2002).

The negative effect of strong winter upwelling on zooplankton abundance may also be explained by (1) advective losses, (2) shrinking habitat due to the rise of the oxycline, or (3) match–mismatch during the succession of upwelling → phytoplankton bloom → zooplankton grazing → zooplankton population growth in developing upwelling lenses and filaments. The theoretical implications and possible mechanisms of prey–predator match–mismatch have been reviewed elsewhere (e.g. Durant et al., 2007). Very strong upwelling may also produce adverse physical–chemical conditions in recently upwelled water (steep temperature gradients, low oxygen, high ammonia concentrations, etc.). This "intermediate upwelling" hypothesis may also be relevant to interannual variability. Accordingly, minimum zooplankton abundance from 1970 to 1976 coincided with long periods with strong La Niña (LN) conditions (Fig. 3), when upwelling intensity was maximal.

The large interannual variability in biomass and species composition off Peru was first shown by Santander (1981). Long-term observations are so far only available as zooplankton volumes (1964–2002; Ayón et al., 2004). The relatively large meshed (300 μm) net used to collect these samples does not quantitatively collect smaller zooplankton that likely dominate the nearshore region. Ongoing research is testing capture efficiencies for smaller mesozooplankton (comparing 300 and 200 μm net catches under different conditions), to determine if biases are stable for given taxa. If so, historical zooplankton collections can be reanalyzed. Carrasco and Lozano (1989) presented abundance data from 1964 to 1987 for the northern, central and southern Peruvian coast and recognized a decline. During the 1983 EN copepod abundance between 6°S and 12°S decreased to 1/6 of values for 1977–1981. Nearer the equator (3–6°S), copepod abundance was higher due to advection of larger equatorial species. Ayón et al. (2004) extended this series to 2002 (Fig. 3). The long-term trend of annual mean zooplankton volume, from 1964 to 2001, displayed three different periods: maximum values from 1964 to 1973, a collapse after 1973, low values from 1974 to 1989 (although the recovery seems to start in 1985), and an intermediate level of biovolumes from 1990 to 2002 (Ayón et al., 2004).



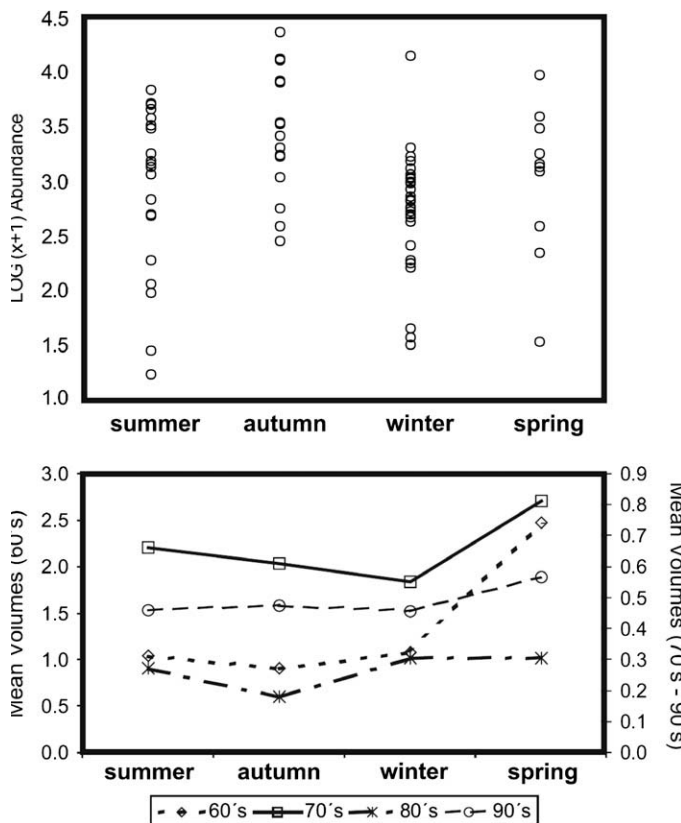**Fig. 2.** Seasonality of zooplankton abundance and biovolumes off Peru. Above: seasonal variation of log total zooplankton abundance off Paita, northern Peru, from August 1994 to December 2004 (modified from Aronés et al., in press). Below: mean seasonal zooplankton volumes off Peru for four decades, since 1964. Note that the scale of the ordinate in the 1960s differs from that of the 1970s and 1990s (Ayón et al., 2004).
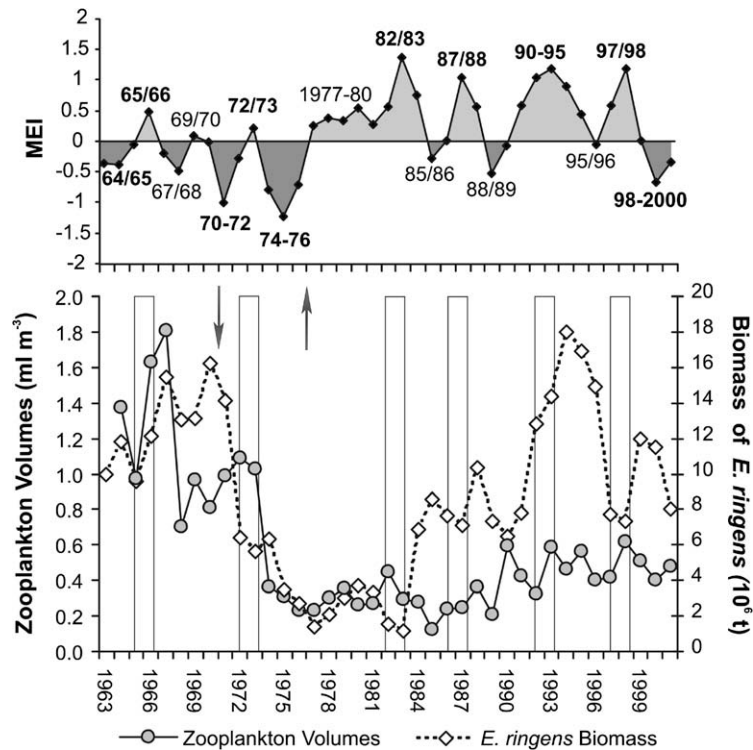
**Fig. 3.** Mean annual tropical Pacific Multivariate ENSO Index (MEI), zooplankton volumes, and biomass of Peruvian anchoveta (*Engraulis ringens*) from 1963 to 2001. Above: the MEI time series shown is the annual average calculated from the original bimonthly MEI series (Wolter and Timlin, 1998). The variables used to calculate the MEI are: sea-level pressure (P), zonal (U) and meridional (V) components of the surface wind, sea surface temperature (S), surface air temperature (A), and total cloudiness fraction of the sky (C). Original data are 2-degree-cells from the tropical Pacific (30°N–30°S) taken from the COADS data base (http://www.icoads.noaa.gov). El Niño periods are highlighted above; La Niña periods are shown below zero. *Source:* http://www.cdc.noaa.gov. Below: average zooplankton volumes from more than 10,000 samples taken from the Peruvian coast to 300 nautical miles offshore. Values of 1979 and 1988 were interpolated with a 5-year moving average [according to Ayón et al. (2004), modified]. Strong El Niño events are shown as vertical bars. Arrows indicate global sea surface temperature regime shifts in 1970–1971 and 1976–1977 (Yasunaka and Hanawa, 2005).

ENSO and multi-decadal shifts in global sea surface temperature (SST) shifts co-occur (Yasunaka and Hanawa, 2005). Although many other strong ENSO transitions occurred since the early 60s, Yasunaka and Hanawa (2005) detected only two global SST regime shifts in this period, one in 1970–1971 (transition from EN to the strong 1970–1972 LN) and another one in 1976–1977 (transition from the strong 74–76 LN to EN conditions). Coincidently or not, these ENSO-related global SST regime shifts mark the beginning collapse of the anchovy stock in the late 60s to early 70s, and onset of stock recovery in the mid 70s (vertical arrows in Fig. 3). The synchrony of the Peruvian zooplankton and anchovy data with statistically significant global SST regime shifts provide further support for the idea of strong links between regional-scale ecosystem changes and global-scale climatic processes.

Zooplankton volumes and anchovy biomass show a similar pattern (Fig. 3), indicating that multi-decadal oscillations may be affecting both compartments of this ecosystem. There may be valid alternative explanations for the variations in anchovy biomass (e.g. overfishing in the late 60s), but the synchronicity of fisheries and zooplankton data in this and other regions of the Pacific strongly indicate a globally relevant ENSO-like multi-decadal oscillation pattern that is probably triggering these ecological regime shifts. However, there are also three remarkable differences between the time series of anchovy biomass and zooplankton volume: (1) the magnitude of the population collapse in the late 60s and early 70s is similar for both anchovy and zooplankton, but the subsequent recovery was much better for anchovies. Zooplankton never recovered 60s levels; (2) strong EN's do not seem to affect zooplankton communities; there is no clear affect of even the strongest EN events on zooplankton volume; (3) the zooplankton

collapse seems to have started 3 or 4 years earlier (in 1968) than for anchovy (in 71 or 72). If real, this association may prove to be a useful early indicator of ecosystem regime shifts. Modelling efforts and time series analyses have shown that mesozooplankton populations respond to subtle climatic signals, and could serve as indicators of climate change (Taylor et al., 2002).

A more recent regime shift in 1999 or 2000 apparently affected pelagic ecosystems in the north-eastern (Greene, 2002; Mackas et al., 2004; Litzow, 2006), north-western (Rebstock and Kang, 2003; Tadokoro et al., 2005), and south-eastern Pacific (Aronés et al., in press). This recent shift, which occurred following the 1997/1998 EN and perhaps during the strong 98/99 LN (Fig. 4), is still under discussion (Bond et al., 2003; Litzow, 2006; Gutiérrez et al., 2007). An analysis of spatial distribution of anchovies and sardines off Peru also showed a dramatic shift after the 1997–1999 ENSO (Gutiérrez et al., 2007). Although sardines were already declining and anchovies had been increasing in biomass before 1999, Gutiérrez et al. (2007) concluded that "since 1999, we have been in a 'full anchovy era' with dramatically low levels of sardine in the HCS". This may be related to an increase in copepod and euphaussiid abundance, which at least off northern Peru, showed an abrupt increase after 1999 (Aronés et al., in press, Fig. 4).

Ayón et al. (2004) and Aronés et al. (in press) demonstrated the importance of long-term zooplankton monitoring in upwelling areas, and confirmed that dramatic changes in pelagic ecosystems occur in the Southeast Pacific. Ayón et al. (2008) used a slightly extended data set (1961–2003) and applied a Generalized Additive Model (GAM) and Classification and Regression Trees (CART) to the zooplankton biovolumes as a function of time of day to examine
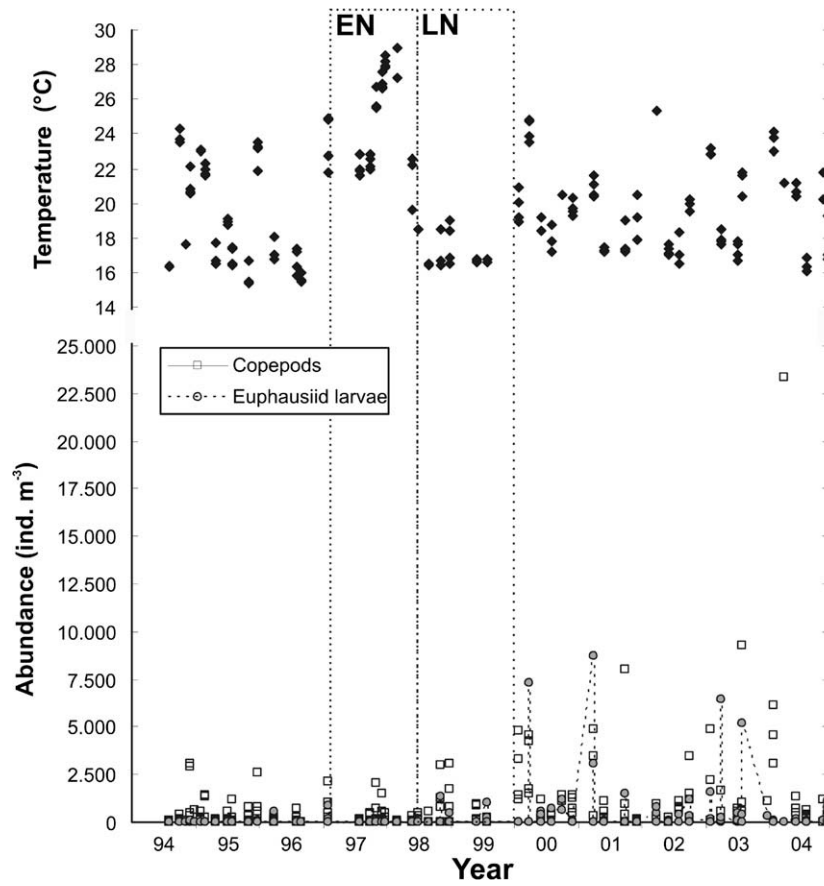
**Fig. 4.** Temporal variation of surface water temperature and subsurface abundance of copepods and euphausiid larvae off Paita, northern Peru, from August 1994 to December 2004. EN, El Niño 1997/1998; LN, La Niña1998/1999. *Source:* Aronés et al. (in press).

the effect of the diel cycle, other environmental factors, and biological interactions on biovolume. The CART results showed a strong negative impact of anchovy but not sardine biomass on zooplankton. Additionally, zooplankton biovolume was higher offshore than on the shelf and was higher when SST was above 21.2 °C for some years and months. GAM results corroborated the CART.

### 4.5. Pelagic macrocrustaceans (Euphausiacea and Decapoda)

Two pelagic macrocrustaceans are characteristic of the Peruvian Humboldt Current System (HCS): *Euphausia mucronata* (or 'krill'; Escribano et al., 2000; Antezana, 2006), and the galatheid crab *Pleuroncodes monodon* ('red crab', 'squat lobster', 'langostino colorado', or 'munida'). These species can be very abundant (Antezana, 2002a,b; Bertrand et al., 2005) and thus likely interact with the even larger biomass of *Engraulis ringens* (Peruvian anchovy). Recent data even indicate that krill may be the main food source for adult anchovy (Espinoza and Bertrand, 2008). Many other predators, such as hake, also feed on these pelagic macrocrustaceans (Mejia et al., 1971, 1973, 1980). Although adults, juveniles, post-larvae and larvae of pelagic decapod shrimps are common in plankton catches in tropical and subtropical oceans (Luciferidae, Sergestidae, Penaeidae, and Caridea; Criales and McGowan, 1994; Schwamborn et al., 1999; Schwamborn et al., 2001; Martins et al., 2005; Koettker and Freire, 2006) and occur off Peru (Fernández-Álamo and Färber-Lorda, 2006, Table 4), there is little information on these groups. Hendricks and Estrada-Navarrete (1989) discussed the distribution of pelagic decapod shrimps in the Eastern Pacific, including offshore waters off Peru, but did not give biomass data for these groups off Peru.

Early euphausiid research focused on taxonomy (Santander, 1967; Santander and Sandoval de Castillo, 1969; Ponomareva,

1982). Although sampling with Hensen nets is probably misses adults, euphausiids were nevertheless found to be very abundant, especially at night (e.g. Santander, 1981). Most euphausiids are captured as furcilia and calyptopis larvae (Aronés et al., in press). Antezana (1978, 2002a,b) studied the distribution of *Euphausia mucronata* along the Peruvian and Chilean coasts and the vertical distribution of developmental stages in relation to the oxygen minimum layer (OML). All stages migrated downward during the day, adults migrating deeper than larvae and juveniles. He suggested that these ontogenetic and diel vertical distribution patterns reflect a predator avoidance strategy and may explain the success of this species, which may contribute up to 50% of total zooplankton biomass in the HCS.

The distribution of red crab extends from Chiloe Island (43°S) off Chile to 7°S off Peru (Haig, 1955; Gutiérrez et al., 2008). Red crab individuals are larger in southern end of their range, where they are mostly benthic (Gallardo et al., 1993; Palma, 1994). Off northern Chile and Peru, red crab individuals are smaller and mostly pelagic (Gutiérrez et al., 2008), leading Rivera and Santander (2005) to consider the northern specimens a "dwarf" subspecies (*P. monodon pelagicus*). Most studies on *P. monodon* have been performed off Chile due to its importance for the fisheries in this region (e.g. Haig, 1955; Palma, 1976; Gutiérrez and Zúñiga, 1977; Bustos et al., 1982; Gallardo et al., 1993, 1994; Palma, 1994; Rivera and Santander, 2005). The biology of red crab in Peruvian waters is not well known (Segura and Castillo, 1996; Chimpén, 1999; Franco, 2003), perhaps because red crab have recently increased in biomass (Gutiérrez et al., 2008). *P. monodon* have been occasionally reported as abundant during the last 50 years, mainly off southern Peru. Older reports indicate that *P. monodon* was an important prey item of tunas during the 1930s and
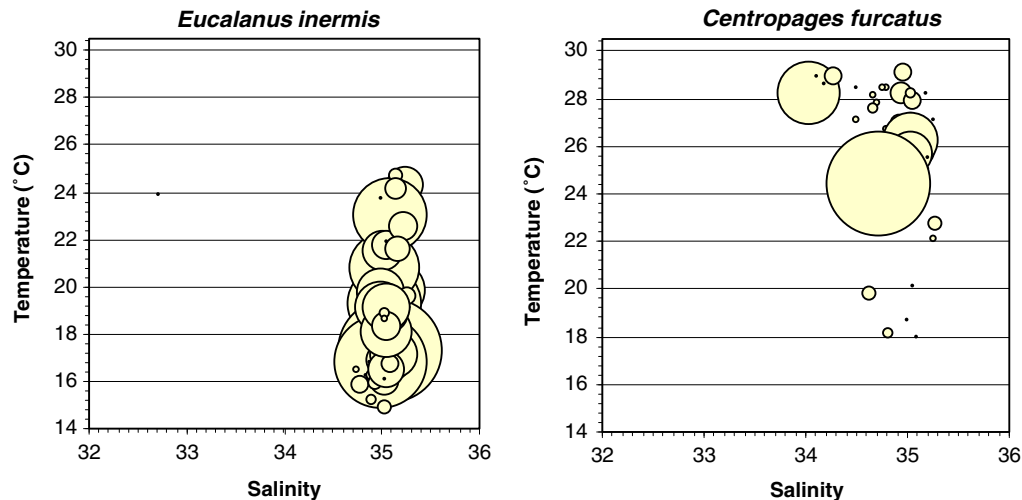
**Fig. 5.** Temperature–salinity diagrams of waters sampled at surface off Callao and San Jose, Peru, from 1994 to 2004, with superimposed abundances of the copepods *Eucalanus inermis* and *Centropages furcatus*. Samples were taken off Callao, San José from 1994 to 2004 with WP-2 hauls. From Abanto, 2001).

1940s. According to Gutiérrez et al. (2008), *P. monodon* became highly abundant along the Peruvian coast after the 1997–1998 EN. Biomass ranged between 0.6 and $3.4 \times 10^6$ t from 1998 to 2005 (acoustic estimates in Gutiérrez et al., 2008) in upwelled nearshore waters where red crab are preyed on by seabirds, mammals, and fish (anchovy preys on red crab zoeae). Gutiérrez et al. (2008) also found that *P. monodon* forage on fish eggs and larvae. Trophic interactions are likely to occur between krill, red crab, and anchoveta.

### 4.6. Meroplankton

Meroplanktonic larvae of benthic invertebrates (e.g. Decapoda, Cirripedia, Mollusca, Polychaeta) constitute an important fraction of the zooplankton, especially nearshore (Criales-Hernández et al., 2008). Although nearshore food supply may be ample, larvae have to cope with predation, advection, and benthic hypoxia. Important predators are planktivorous fishes and macrocrustaceans, which build up huge biomass in this region. Surface currents in coastal upwelling regions are, on average, directed alongshore or offshore and subsurface waters are anoxic, thus limiting any vertical migration (Shanks and Brink, 2005). Variability in currents exists at various scales, including the upwelling/relaxation cycles, EN and decadal cycles. Shallow-water invertebrates must be able to recruit from larvae retained nearshore or in bays, or, as postulated by Pielou (1975), follow an r-strategy and produce huge numbers of larvae, few few of whom return to shore.

The meroplanktonic larvae of many commercially important benthic organisms remain largely undescribed. The distribution of pelecypod larvae has been described for two cruises in Bahia de Independencia (Mendo et al., 1989; Yamashiro et al., 1990). Increased survival and recruitment of larvae probably explain the dramatic population increases of the scallop *Argopecten purpuratus* that occur during EN. One explanation for "scallop outbursts" is that larval survival increases with temperature (Wolff et al., 2006) and a thicker surface oxic layer, while another idea is that larval predators or competitors disappear from surface waters during EN (e.g. anchovy and crab larvae). Tarazona et al. (1988) studied the bivalve communities of the central Peruvian coast during the 1982–1983 EN. Abundance of bivalve larvae declined during peak EN months in 1983, but recovered immediately afterwards. The meroplankton of Ancón Bay (11°46′S 77°11′W) and Independencia Bay (14°09′S 76°10′W) (Fig. 1) were compared by Tarazona

et al. (1989), who found that polychaete larvae dominated Independencia Bay, while bivalve larvae dominated Ancón Bay. Experiments showed that in spite of small tidal amplitude (<1 m), tidal currents dispersed larvae. Scallop larvae may can occur in huge densities nearshore, specifically in Independencia Bay (M. Wolff, personal communication). Yamashiro et al. (1990) evaluated larval stocks in Independencia Bay. The meroplankton was comprised of brachyuran zoeae, brachiopod, gastropod, and polychaete larvae, together with young pteropods and euphausiid larvae. Tidal fluctuations in larval abundance were also observed. Macro-invertebrate settlement in this bay during the 1997–1998 EN has been described by Ramos et al. (1999) by determining recruitment to artificial substrates. *Argopecten purpuratus* only settled during EN, together with warm water turriform gastropods. In contrast, the bivalve *Hiatella solida*, the turbellarian *Notoplana* sp., and the gastropod *Caecum chilense* settled mainly during the preceding cold period. A third group, comprised by the brachiopod *Discinisca lamellosa*, the echinoderm *Ophiactis kroyeri*, and mytilid bivalves, settled only at the very onset of EN (March 1997). This EN-onset settlement peak may be related to unusually strong onshore currents associated with a month-long relaxation of upwelling, or to ecosystem changes. The appearance of unusual tropical species at the end of this EN were also noted (e.g. the bivalve *Pteria sterna* and the gastropod *Epitonium* sp.). Further studies on macro-invertebrate settlement in Peruvian inshore ecosystems have recently been published by Pacheco and Garate (2005).

Larval development has been described for less than 10% of the decapod species that occur off Peru, mostly from other parts of the eastern Pacific (e.g. Costlow and Fagetti, 1967; Quintana, 1983; Dittel and Epifanio, 1984; Quintana and Saelzer, 1986; Báez and Martín, 1992; Báez, 1997; Wehrtmann and Báez, 1997). Although crab larval stages are generally found in zooplankton surveys, there are no species-specific data on decapod larval distributions off Peru. This is one of the focuses in the ongoing CENSOR project.

### 4.7. Trophodynamics and production of zooplankton

Dugdale and Goering (1970) first studied the trophic role of zooplankton in the Peruvian HCS. Their study of biological production in the Peru Coastal Current during a period of high diatom levels indicated grazing was not the principal source of loss of phytoplankton, with combined anchovy and zooplankton grazing at about 20% of the standing crop. They also suggested that the

anchovy were more important grazers than zooplankton. Beers et al. (1971) estimated the consumption by the zooplankton not to exceed 25% of the daily primary production.

During the cruises of the Institute of Oceanology in 1974, attempts were made to describe plankton community dynamics (Vinogradov and Shushkina, 1978; Flint and Timonin, 1985) and to estimate zooplankton production (Shushkina and Kislyakov, 1977). Drits (1985) measured the ingestion rate of *Calanus australis* under natural conditions and studied the content of the gut and faecal pellets. Mikheyev (1977a) described the age structure of dominant copepod species on a transect across the shelf and an upwelling center and compared species number, biomass and species diversity (Mikheyev, 1977b). Flint and Timonin (1985) assessed trophic structure of the crustacean community using mouthpart morphology. In nearshore areas, fine filter-feeders dominated. Over the shelf break area, they found a predominance of coarse filter-feeders and omnivores. Spatial variability in the zooplankton community was explained by the patchy distribution of local upwelling cells, which undergo characteristic changes depending on their age. Secondary production was from experiments following the fate of $^{14}$C-labelled phytoplankton and applying a mathematical simulation of a trophic model (Shushkina and Kislyakov, 1977). According to Petipa et al. (1977) excess production on the shelf is utilized in a 200–300 km band of offshore water.

Measurements of grazing and excretion rates of copepods and qualitative descriptions of their prey were conducted during the international projects ICANE and CUEA. According to Cowles (1978, 1979), prey size selection by copepods depended food abundance. Smith et al. (1981a,b) measured ingestion rates of *Acartia tonsa*. Dagg et al. (1980) measured rates of ingestion and excretion of *Calanus chilensis*, *Eucalanus inermis*, and *Centropages brachiatus*, assessing the particle spectrum with a Coulter Counter. As these large species ingested <5% of primary production, the authors suggested that smaller zooplankton must consume most primary production. Boyd et al. (1980) studied prey selectivity by *Eucalanus*, *Calanus*, and *Centropages*. They found that *Calanus* sp. is a non-selective phytophage, while *Centropages* sp. and *Eucalanus* sp. were omnivorous feeders. Furthermore, *Eucalanus* sp. did not feed at the surface at night, but only during the day on OMZ detritus. Nitrogen regeneration during a red tide was measured by Smith (1978), who estimated that mesozooplankton recycled 1–25% of the nitrogen needed to support phytoplankton production. Espinoza and Bertrand (2008) have recently emphasized that in carbon units, anchovies feed primarily on euphausids (66%) and copepods (28%), not diatoms as has traditionally been thought (Pauly et al., 1989).

### 4.8. Modelling

The first ecological models of the HCS were built by Dugdale and MacIsaac (1971) and Walsh and Dugdale (1971), who simulated nitrate uptake and flow through the Peruvian upwelling system. Energy budgets for the pelagic system were established by Sorokin and Mikheev (1979), using data obtained during the cruises of the Institute of Oceanology in 1974. Walsh (1981) established a carbon budget to understand changes in the carbon flow through the coastal upwelling system after the crash of the anchovy fisheries in the early 70s. Jarre et al. (1991) presented mass balance models (ECOPATH II) for modeling fish stock interactions in the Peruvian upwelling ecosystem, which included also a zooplankton component. Jarre-Teichmann (1998) investigated explored trophic structure with steady-state, mass-balance models (ECOPATH II). The mean transfer efficiency from herbivores to top predators was 4–6%. Comparison of the models for the warm sardine regime versus the cold anchovy regime suggested that anchovy abundance varies with the lower components of the ecosys-

tem (zooplankton and, to some extent, phytoplankton and detritus), while sardine abundance is out of phase. Jarre-Teichmann (1998) concluded that mobility differences between the two species, with sardines relying on their better swimming capability (Bakun and Broad, 2003) to find suitable forage during periods of decreased productivity at lower trophic levels. However, more recent studies emphasize that the major reason for alternation anchovy and sardine abundance is due to is climatic and prey selection mediated (with sardines feeding on phytoplankton and small-sized zooplankton and anchovies on larger copepods and euphausiids), and not related to swimming capability (Bertrand et al., 2004; Gerlotto et al., 2006; van der Lingen et al., 2006; Espinoza and Bertrand, 2008).

Carr (2003) used a numerical model to quantify carbon flow through the upwelling ecosystem from 1996 through 1998 at 9.5° off the coast of Peru. The numerical experiments illustrate ecosystem responses to the evolving conditions associated with EN and LN events.

Ecosystem modelling in the Peruvian upwelling system is only beginning. There is a strong need for theoretical overview, and empirical data is needed as model input. Due to the lack of data, e.g. on the microbial loop, macrocrustaceans and main trophic links, e.g. between anchovies and euphausiids, older models neglect important ecosystem components. Recent trophic models built using the Ecopath with Ecosim (EwE) software focus mainly on commercially important fish and invertebrate stocks. These models do include more recent stomach content data for anchovy (Tam et al., 2006; Taylor et al., 2006; Wolff et al., 2006), yet phytoplankton–zooplankton interactions are not well described and the microbial loop has not yet been integrated. Recent physical–biogeochemical simulations (Echevin et al., 2004b) also do not consider phytoplankton–zooplankton interactions, again showing the need for new data and modelling directed specifically towards the plankton.

## 5. Knowledge gaps and perspectives

Many topics in zooplankton biology and ecology have been examined off Peru, but a synthetic view of zooplankton dynamics in this part of the HCS and its relation to other components of the system has not yet emerged. There are many important issues still poorly understood, such as the interactions of gelatinous and crustacean plankton, adaptations to life in the OML, microzooplankton dynamics and processes related to the microbial loop. Most urgently, we need concepts, data, and models which may help to link climatic processes to the productivity of the pelagic ecosystem off Peru.

### 5.1. Taxonomy, life cycles, and cryptic taxa

Taxonomy of zooplankton off Peru is still in its infancy. There is a strong need to combine morphological and genetic studies and compare species with their synonyms in other oceans. Furthermore, little to nothing is known of the ecology of most species. Often, developmental stages of holo- and meroplankton are not described. Basic knowledge of the life cycles is lacking, such as generation times and growth rates, reproductive biology, starvation potential, and life cycle strategies such as dormancy and resting eggs.

Euphausiids may form a large part of the zooplankton biomass. However, due to difficulties in sampling, their biomass may be significantly underestimated. Similarly, gelatinous plankton is often very abundant, but requires dedicated sampling techniques to quantitatively assess its importance. There is little knowledge on bentho-pelagic coupling and the role of meroplankton, especially

in the nearshore zone, which is important for artisanal fisheries. This is one of the main focuses of the ongoing CENSOR project.

## 5.2. Microzooplankton and the microbial loop

The microzooplankton comprises organisms <200 μm (UNESCO, 1968; Smith, 1977; Lenz, 2000), and are typically dominated by protozoa (rotifers, foraminiferans, radiolarians, ciliates, and flagellates) and copepod eggs and nauplii. Protozoan communities are often mixotrophic or of unknown trophic status. They are generally not caught by zooplankton nets, but may be quantified in bacterio- and phytoplankton studies, which may lead to a considerable overlap between bacterio-, phyto-, and zooplankton studies regarding these groups. Microzooplankton can be intense grazers on bacteria and phytoplankton with extremely high production/biomass ratios (Kiørboe, 1997; Agis et al., 2007; McManus et al., 2007), however, little is known about its role off Peru, although it is certainly important, especially during EN, as shown by studies in the adjacent southern HCS (Escribano et al., 2004).

The few studies available are all based on single cruises, usually with few stations. Tumantseva and Kopylov (1985a,b) determined the species composition and biomass of planktonic protozoa and their rates of reproduction and production off Peru. In incubation experiments the average P/B ratio was 1.26 day$^{-1}$, indicating biomass was more than doubling each day. *Urotricha marina* underwent 8–11 divisions/day. Vinogradov et al. (1980) found similar results and pointed out the importance of microzooplankton production. Heterotrophic microplankton was also studied by Sorokin (1978) and Klekowski et al. (1975), who determined respiration rates of microzooplankton in the equatorial and Peruvian upwelling systems. Sorokin and Kogelschatz (1979) studied the role of heterotrophic microplankton in the flux of organic matter to the benthos near Punta San Juan, Peru. A drogue study showed that the planktonic community in freshly upwelled water was dominated by microheterotrophic bacteria and protozoans, where bacteria (49 mg C m$^{-3}$) exceeded by two orders of magnitude the biomass of phytoplankton. Total oxygen used by microheterotrophs exceeded by three-times that produced by primary production, indicating that the heterotrophic respiration was dependent on organic matter pre-existing in the upwelling waters. Tintinnids and their relation to EN were studied by Gómez (1997). The pelagic ecosystem of the equatorial upwelling, including bacteria, several size fractions of phytoplankton, micro- and mesozooplankton, was analyzed by Vinagradov et al. (1977).

Clearly, the studies mentioned above are not nearly sufficient to give even a superficial picture of the processes involving microzooplankton and the microbial loop in the waters off Peru. This shows the urgent need for further studies as to improve our understanding of its highly productive ecosystem.

## 5.3. Perspectives and suggestions for data acquisition

As it now exists, the Peruvian zooplankton time series is most valuable, and must continue with a consistent methodology and strategy (Table 2). Such time series are essential to study relationships between climate and ecosystems. However, biovolume data alone are often not sufficient to understand regime shifts and their consequences for higher trophic levels. More information is needed on taxonomic composition or at least on size spectra. For estimates of trophic transfer a common unit for biomass (dry mass, carbon content) is essential.

For the short term, the addition of modern optical and acoustical zooplankton sensors to standard large-scale surveys will vastly improve our description of the spatial distribution of zooplankton. The new CRIOS cruises (Table 2) provide a regular monitoring of primary and secondary production and mesozooplankton grazing. These cruises also provide excellent opportunities for process studies (e.g. microbial loop, microzooplankton grazing, the effects of red tides and diatom blooms on zooplankton population dynamics, physical and trophic processes in fronts and upwelling filaments, etc.).

On the long-term, new strategies for data acquisition in real time may yield new perspectives on the dynamics of the Peruvian upwelling ecosystem. To better understand the links between climate and fish, all components of the pelagic system including zooplankton have to be considered, preferably by synchronous interdisciplinary efforts. Still, little is known about many dynamic processes that characterize upwelling systems, such as the evolution of biological communities within upwelled cells. The scale of events controlling the biological–physical interaction is not clear yet. To construct models which effectively encompass the size of the system actually in operation requires at the very least a spectral analysis of the environmental events from the order of days to months, and eventually to years. A powerful device to obtain such information would be an array of autonomous sensors (current meters, ctdo, fluorescence probe, acoustical and optical plankton counters) anchored at appropriate locations along the shelf (Dickie and Valdivia, 1981). Process studies could then be embedded in such a mooring array.

The use of autonomous profiling floats (Roemmich et al., 2004), autonomous underwater vehicles (AUVs, Curtin et al., 1993; Griffiths et al., 2000; Samson et al., 2001; Yu et al., 2002) and enduring autonomous gliders (Sherman et al., 2001; Rudnick et al., 2004) together with satellite imagery may be an additional possibility to generate long-term high-resolution data on important physical, biogeochemical, and biological variables.

## 5.4. Models

Little attention has been given to the stochastic nature of upwelling systems (Menshutkin et al., 1980), that are influenced by random events that make them shift unpredictably between multiple states (e.g. upwelling and relaxation, red tides versus diatom blooms, etc.). Considering this stochastic nature, early statistical descriptions of meteorological, oceanographic, and fisheries data have concluded that predicting the states of the Peruvian upwelling ecosystem "longer than some months ahead may be beyond reach" (Bohle-Carbonell, 1989). This rather pessimistic view was largely true in the 1970s, considering the unexplained collapse of the anchovy fisheries and ignorance of ENSO and multi-decadal cycles.

Recently, considerable progress has been made in forecasting ENSO (e.g. Penland and Matrosova, 2001; Chen et al., 2004; Cash et al., 2006) and in understanding the intrinsic relationship between ENSO and multi-decadal cycles (Yasunaka and Hanawa, 2005; Ye and Hsieh, 2006). Individual-based Lagrangian models can integrate physical, biogeochemical and biological data (Leising and Franks, 2000; Woods et al., 2005; Croquette and Eldin, 2006). However, only recently this approach has been applied to model zooplankton advection in coastal upwelling regions (Batchelder et al., 2002; Carr et al., 2008). Ecosystem modelling should focus on predicting how future cyclic (e.g. ENSO and multi-decadal variation) and non-cyclic changes (e.g. global warming and ocean acidification) will affect upwelling ecosystems.

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